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headwater streams for regional diversity

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TROPICAL STREAM DIATOM COMMUNITIES — THE IMPORTANCE OF HEADWATER STREAMS FOR REGIONAL DIVERSITY

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Abstract

Understanding how species are distributed in space and time is a focal element guiding conservational efforts under the ongoing climate change and Holocene extinction. Freshwater habitats are currently one of the most threatened ecosystem types and studies aiming to unravel factors that govern biodiversity of tropical stream micro-organisms are especially scarce. Diatoms play an important role as primary producers in streams and are widely used as ecological indicators. Yet, relatively little is known about which factors affect diatom communities in the tropics.

Here, we studied benthic diatom diversity across 67 tropical streams spanning stream orders 1 – 5 in Kenya. We examined whether the hypothesis of latitudinal diversity gradient applies for benthic diatoms, i.e. do tropical streams encompass more species than boreal streams using comparable boreal dataset. In addition, we studied which environmental, land use and spatial factors control benthic diatom communities using redundancy analysis. We also examined the nestedness and turnover components of beta diversity, factors contributing to diatom species richness and the uniqueness of the communities across stream orders by using boosted regression trees and local contribution to beta diversity. Finally, we studied whether environmental heterogeneity and beta diversity are related across stream orders and tested their relationship using tests of homogeneity of dispersion and regression analysis.

Species richness was not higher in tropical streams than in boreal ones. Tropical diatom communities were controlled jointly by local environmental and spatial factors. Although water chemistry was the most important controlling factor, also physical variables contributed significantly to community variation. Land use had also a significant effect on diatom communities as broad leaved forest streams harboured different diatom communities compared to streams with higher human impact and conductivity, stressing the importance of forests to water quality and diatom biodiversity. Headwater streams encompassed highest species turnover, whereas nestedness was higher in higher order

streams. Species richness was significantly higher in higher order streams than in headwaters, whereas the uniqueness of the communities peaked in headwaters. Environmental heterogeneity was the highest in headwater streams and was related with high beta diversity, which highlights the importance of habitat heterogeneity to biodiversity. Our results stress the management and conservational importance of headwater streams and tropical montane forests as these environments harbour unique diatom communities important for regional diversity.

Keywords: beta diversity, community structure, diatoms, environmental heterogeneity, headwaters, tropics

1. Introduction

How species are distributed across Earth in space and time remains a fundamental topic guiding conservation efforts under the ongoing climate change and Holocene extinction (Pimm *et al*., 1995; Thomas *et al*., 2004). Extinction threat concerns not only terrestrial ecosystems but also aquatic communities. Freshwater habitats harbour disproportionally large species richness in relation to habitat area in many taxonomic groups and freshwater biodiversity is more threatened than biodiversity in other ecosystems (IUCN, 2009; Strayer and Dudgeon, 2010; Wiens, 2016). Thus, understanding of the drivers that maintain species diversity is urgently needed in order to combat severe biodiversity losses taking place at present.

While studies aiming to unravel the determinants of macro-organismal biodiversity have been extensive (Rosenzweig, 1995), microbial communities (e.g. bacteria, unicellular algae and fungi) have received less attention in this regard (Green *et al*., 2004; Zeglin, 2015). For example, whereas

latitudinal diversity gradients are well documented for macro-organisms (Gaston, 2000; Hillebrand, 2004; Lawton, 1999), the existence of such pattern for micro-organisms remains a controversial issue (Hillebrand and Azovsky, 2001; Passy, 2010; Salinas *et al*., 2015). Furthermore, microbial biodiversity studies in boreal and temperate regions have been far more numerous than in the tropics but see for example (Bellinger *et al*., 2006; Bere, 2014; Bojorge-Garcia *et al*., 2014; Mangadze *et al*., 2015).

The diversity and composition of microbial communities are affected by a wide range of determinants and there is still no consensus whether the key drivers are more related to the local environment (Gothe *et al*., 2013; Maloufi *et al*., 2016) or spatial factors (Crump *et al*., 2007; Soininen *et al*., 2004). Also land use (Bere and Tundisi, 2011; Carpenter and Waite, 2000) or climatic factors (Pajunen *et al*., 2016) may affect aquatic microbial communities. Finally, spatial scale of the study influences the factors which govern microbial communities (Lindstrom and Langenheder, 2012) and communities may thus often be described by the shared influence of spatial and environmental factors with increasing spatial influence in larger studies (Heino *et al*., 2014; Soininen *et al*., 2016; Verleyen *et al*., 2009).

Freshwater organisms may be especially vulnerable to changes in precipitation and possible droughts can quickly alter the freshwater habitat and thus their biodiversity (Wiens, 2016). Streams encompass disproportionately high biodiversity (Vinson and Hawkins, 1998; Vorosmarty *et al*., 2010) and stream network provides an excellent environment to study diversity patterns via its hierarchic dendritic organization (Grant *et al*., 2007). River Continuum Concept (RCC) predicts biological diversity to peak at mid-order streams, whereas headwaters and large rivers should be less diverse (Vannote, 1980). However, while this prediction might hold true for alpha (local) diversity, beta (between-site) and gamma (regional) diversity may show different patterns as especially headwater streams (orders 1–2) may harbour a great proportion of biodiversity compared to higher order stream branches (Meyer *et al*., 2007). Moreover, human induced disturbances usually increase with increasing stream order

(Januchowski-Hartley *et al*., 2011), which may affect biodiversity. Headwater streams may also be more physically variable promoting environmental heterogeneity and subsequently also beta diversity (Finn *et al*., 2011). Consequently, possible environmental homogenisation in higher order streams may decrease beta diversity compared to headwaters.

High beta diversity in headwaters may also be caused partly by the more isolated position of headwater streams compared to higher order branches (Finn *et al*., 2011). Thus, highly connected sites at lower reaches harbour lower beta diversity due to higher exchange of individuals between sites leading to homogenisation of communities (Lopes *et al*., 2014). Furthermore, anthropogenic and natural stressors may cause different patterns to beta diversity given that beta diversity under natural disturbances may be caused more by species turnover (i.e. the shared number of species between sites is small), whereas community dissimilarities under anthropogenic stressors may be more generated by nestedness (i.e. poorer assemblages are subsets of those of richer sites) (Gutierrez-Canovas *et al*., 2013). These patterns are largely unresolved in tropics, however, as stream beta diversity has not been studied extensively in tropical regions (but see (Al-Shami *et al*., 2013; Tonkin *et al*., 2016) and microbial communities have received even less attention.

Sub-Saharan Africa is going through an intense land cover change due to human population growth and subsequent cuts of forests into arable land (Brink *et al*., 2014; Pellikka *et al*. 2017a). Land cover changes can have severe effects to the environment and natural resources (Alcantara-Ayala *et al*., 2006; Hohenthal *et al*., 2015). Furthermore, land use changes in the catchments may have profound effects also on aquatic ecosystems via water scarcity, increased turbidity and nutrient fluxes (Allan and Castillo, 2007; Hohenthal *et al*., 2015; Soininen *et al*., 2015). Human impact on stream communities usually grow downstream, agricultural effects causing the most severe threat to biodiversity (US - Environmental Protection Agency, 2000; Vorosmarty *et al*., 2010). The detrimental anthropogenic effects are increased by the poor waste water treatment in many rural areas (Concoran

et al., 2010). Indeed, freshwater biodiversity conservation under the increasing human demands of water poses a true challenge (UNESCO, 2009; Wiens, 2016; Vorosmarty *et al*., 2010).

Benthic diatoms are a pivotal component of stream biodiversity and are widely used as ecological indicators (Hill *et al*., 2000; Wang *et al*., 2005). We studied the diversity and composition of stream benthic diatom communities in Taita Hills, Kenya. The area is considered as a biodiversity hotspot with a high rate of endemism of plants (Beentje and Ndiang'ui, 1988; Gereau *et al*., 2006; Lovett and Wasser, 1993) and animals (Gereau *et al*., 2006). At the same time, however, the area is affected by intensive land use change along with other anthropogenic pressures threatening ecosystems and their functioning (Pellikka *et al*., 2013; Pellikka *et al*., 2009). First (Q_1), we were interested if there are major richness differences between tropical and boreal stream diatoms. We thus compared diatom species richness between tropical and boreal streams using two data sets with identical sampling methods. We expected that species richness is higher in tropics as found for other taxa (Hillebrand, 2004). Second (Q_2), we studied the effects of local environmental, land use and spatial factors on tropical stream diatom community composition. We expected water chemistry and stream physical variables to have a significant effect on diatom composition (Soininen, 2007) but also that communities are spatially structured (Piano *et al*., 2017). In addition, we expected land use to affect diatom communities indirectly via affecting water quality (Bere and Tundisi, 2011; Carpenter and Waite, 2000; Potapova and Charles, 2002). We considered the use of the diatoms and their diversity as ecological indicators of land cover change by sampling diatoms in four massifs of the Taita Hills of Kenya, which differ in their land use history, but are similar in their bedrock, soil types, forest species composition, agricultural crop composition and climate. Thirdly (Q_3), we studied the distribution of diatom biodiversity across stream orders. We expected headwater sites (orders 1–2) to harbour more unique diatom communities, and simultaneously, to have lower species richness than higher stream order sites (Meyer *et al*., 2007; Sherwood *et al*., 2000). We also examined beta diversity components, i.e., species turnover and nestedness across stream orders and expected species turnover

to be largest in headwaters while nestedness to be largest in downstream sites. Fourthly (Q_4), we examined factors contributing to diatom species richness and the uniqueness of the communities. We expected that species richness is mostly related to conductivity (Heino *et al*., 2010) and pH (Jyrkänkallio-Mikkola *et al*., 2017) whereas uniqueness would be most related to conductivity and nutrient levels (Pajunen *et al*., 2017). Finally (Q_5), we studied whether environmental heterogeneity and diatom beta diversity are related across stream orders and tested their relationship. We expected headwater streams to harbour higher beta diversity and environmental heterogeneity (Finn *et al*., 2011; Meyer *et al*., 2007) than sites at higher order streams.

In this study, we characterized diatom communities using species richness, community composition and the uniqueness of species composition at sites, measured as local contribution to beta diversity (LCBD; (Legendre and De Caceres, 2013). Since beta diversity provides the most useful measure to understand the processes that generate and maintain biodiversity (Legendre *et al*., 2005; Qiao *et al*., 2015; Socolar *et al*., 2016) we placed most emphasis on beta (between site) diversity in terms of dissimilarities and local contribution to beta diversity.

2. Material and methods

2.1. Study area

Taita Hills is the northernmost part of the biodiversity hotspot Eastern Arc located in southeastern Kenya rising in the middle of plains to hilltops over 2000 m of an altitude (Platts *et al*., 2011). Taita Hills can be separated to Dabida massif, Mbololo massif, Sagala Hill and Mt. Kasigau, which are within 40 km from each other. The mean elevation of Dabida is between 1300 to 1600 m a.s.l., the highest peaks reaching over 2000 m a.s.l. Mbololo massif reaching 1800 m is located east from Dabida separated by Paranga valley at 900 m a.s.l. Sagala Hill reaching 1500 m a.s.l. is located 15 km southeast from Dabida and Mbololo, and Mt. Kasigau reaching 1600 m a.s.l. at 40 km southeast

156 from Dabida (Fig. 1). Located in the intertropical convergence zone Taita Hills face bimodal rain
157 pattern having rainy season in November-December and in March-May. Annual rainfall in the hills
158 is normally 1200 mm, while the lowlands receive less than 600 mm per year resulting to rule of the
159 thumb that higher elevations have higher rainfall and are covered more by forests than lower
160 elevations (Erdogan *et al*., 2011). However, as the rains are orographic in nature, the eastern slopes
161 and hills of Mbololo and Dabida receive more precipitation than the leeward parts and slopes located
162 in the west. A significant addition to the precipitation is occult precipitation, which is estimated to
163 result in 20% addition to precipitation, but only in the forests as forest volume is required to capture
164 the atmospheric moisture, the mist (Pellikka *et al*, 2017b).

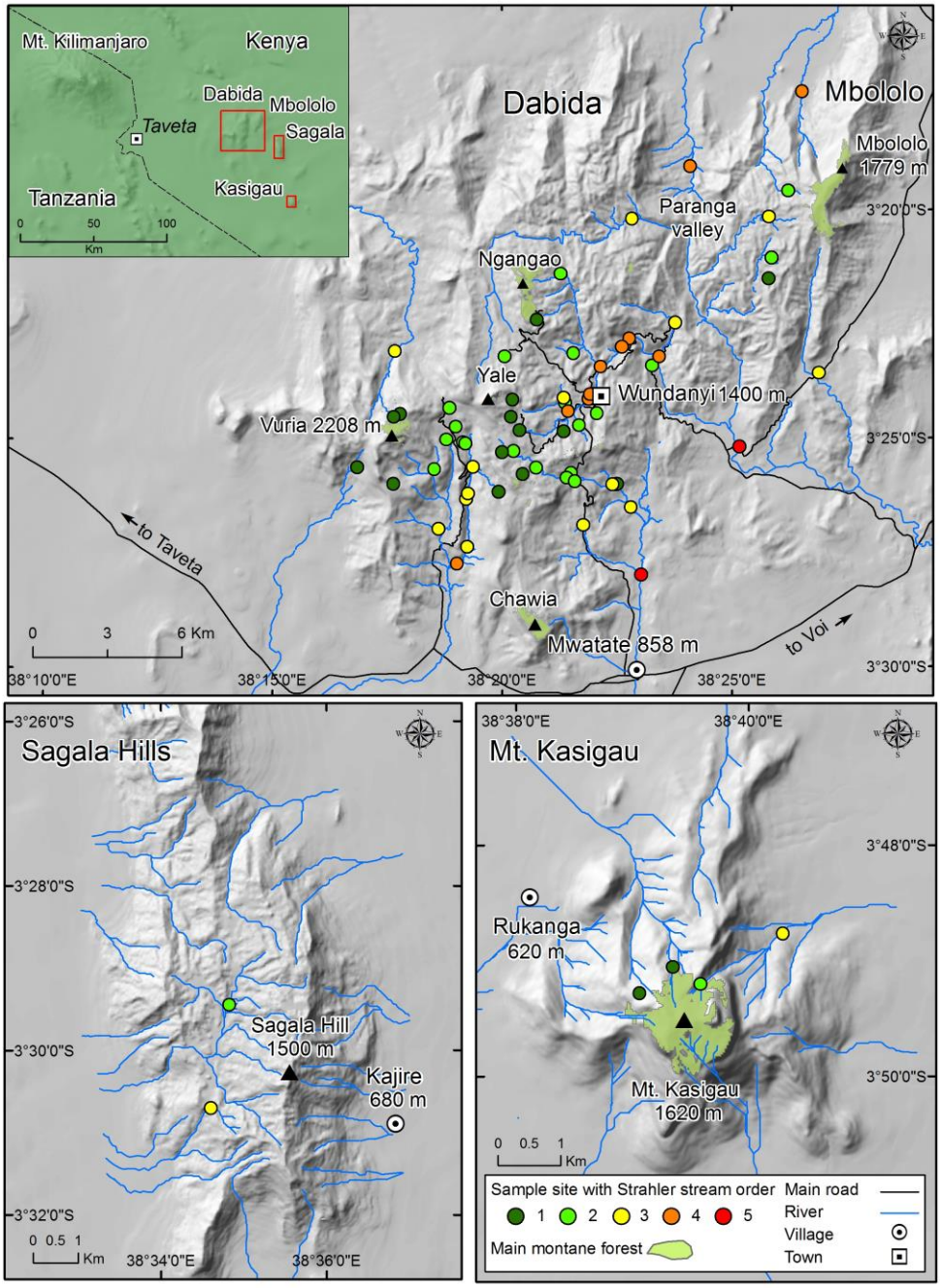


Figure 1 Map of the sampling area

It is estimated that the hills over approximately 1220 m a.s.l. prior human disturbance were covered by forests characterized as evergreen moist lower or upper montane forests. Now only a few percent of the montane forests are left mainly as protected forests managed by Kenya Forest Service. Below 1220 m a.s.l. the forests can be characterized as Acacia-Commiphora woodland, which is partly deciduous depending on the species. The hills are cleared for intensive small-scale agriculture the

main crop being maize producing to harvest per year (Jaetzold and Schmidt, 1987). The lowlands are used for dryland farming, grazing by goats and camels, sisal plantations and conservation areas.

The four massifs studied differ in their land use. Based on Pellikka *et al*. 2017a, only the hilltops of Dabida and Mbololo massifs are covered by montane forests. Due to cloudy conditions, the peak of Vuria (2208 m a.s.l.) is characterized as upper montane forest, elfin forest, with trees covered heavily by epiphytes (Stam *et al*., 2017), while the other native forests are lower montane forests with less epiphytes, but trees reaching up to 40 m of a height. Over 1220 m a.s.l. in 241 km^2 of an area, croplands cover nowadays 40.4 %, montane forests 3.2 % and plantation forests of mainly pine and eucalyptus 10.1%, and woodland, shrubland and thickets all together 44.8% (Pellikka *et al*. 2017a). The remaining fragments of montane forests in Dabida and Mbololo massifs are 1–2 km^2 in size: Mbololo (185 ha), Ngangao (120 ha), Vuria (ha) and Chawia (86 ha) being the largest ones. These forests are all degraded due to selective timber harvesting and grazing inside of the forest, especially in Vuria and Chawia. The least degraded is Mbololo forest and then Ngangao (Omoro *et al*., 2013).

Sagala hill has no native montane forests left, but has some plantation forests and degraded woodlands. The montane forest of Mt. Kasigau can be characterized as upper montane forest over 1500 m a.s.l. due to misty conditions producing fog deposit, and lower montane forest down to 1000 m a.s.l. (Medley and Maingi, 2014) below which dryland forest like Acacia-Commiphora with Euphorbia ssp. takes place. The montane forest of Kasigau is least disturbed of all the forests of the Taita Hills being 2.03 km^2 in size (Medley and Maingi, 2014). Croplands did exist in Mt. Kasigau few decades ago, but were abandoned in order to safeguard water resources (Rikkinen *et al*., 2015). Evidently due to very steep slopes they were also difficult to manage (Adhikari *et al*. submitted).

2.2. Biological data collection

Diatom samples were collected at 67 sites from all four mountain massifs (Fig.1). Sampling was completed in three weeks in January 2016. Diatoms were sampled by randomly selecting and brushing 10 cobble-sized stones or bedrock. The samples were collected from different part of the stream site in order to control small-scale variability in the community composition. To standardize the sampling area we used a 5 × 5 cm rubber template. The samples were preserved with 99% ethanol and stored at +4 °C. Wet combustion with hydrogen peroxide (20%, H_2O_2) was used to clean diatom frustules from organic material. Subsequently, samples were mounted on microscope slides using high-refractive mounting resin Naphrax. We counted and identified at least 500 frustules from each sample using phase contrast light microscope with 1000 × magnification. Species identification was based on Krammer and Lange-Bertalot (1986-1991) and Taylor *et al*. (2007).

2.3. Chemical and physical measurements

Water samples for total nitrogen, total phosphorus and water colour were collected a few meters upstream from each sampling site. Total nitrogen was determined by using alkaline persulfate digestion where alkaline oxidation is carried out in a thermo digester and the converted total nitrogen quantified colorimetrically. Total phosphorus was determined by inductively coupled plasma-optical emission spectrometry (ICP-OES). However, as the method lacked the sensitivity to determine phosphorus concentrations below 10 µg L^{-1} and the phosphorus content of 51 samples were ≤ 10 µg L^{-1} we were unable to use total phosphorus in the following analyses. Water colour was analysed using standardized method (EN ISO7997).

To measure conductivity, pH and temperature in the field we used YSI professional plus water quality meter (YSI Incorporated, Yellow Springs, USA). Current velocity was measured with Schiltknecht MiniAir 2 flow meter (Schiltknecht, Gossau, Switzerland) from 30 locations covering the sampling

site extensively. Water depth was similarly measured from 30 locations and stream width from 10 locations covering the length of the whole sampling site.

Substratum particle size was measured from 10 locations using a 50 × 50 cm quadrat placed in random sites on the streambed. We used a modified Wentworth scale to visually classify the substratum particle size: sand (diameter 0.25 mm – 2 mm), gravel (2 mm – 16 mm), pebble (16 mm – 64 mm), cobble (64 mm – 256 mm) and boulder (>256 mm) (Wentworth, 1922). Canopy shading was individually estimated from 20 locations covering the whole sampling site. Range and average values of measured environmental variables are listed in Appendix A in the supplementary material.

2.4. Stream order analyses and land cover data

River network and stream ordering were calculated from Digital Elevation Model (DEM) data. DEM of 1 × 1 m resolution was derived from airborne laser scanning (ALS) data sets for two parts of the study area (Taita Hills and Kasigau). Laser scanning data was acquired in 2013 and 2014 (using Optech ALTM 3100), and data was filtered for buildings, powerlines and outliers using Terrascan software (Terrasolid Oy), LasTools (Rapidlasso GmbH) and manual editing. For Sagala area, a DEM was created from scanned Survey of Kenya 1:50 000 scale topographic map from which the contour lines were digitized and converted to 10 m resolution raster DEM.

Watershed delineation was based on the DEM layers and, hydrological modelling tools in ArcGIS 10.3.1. Firstly, elevation grids were filled to create a surface that has no sinks. Then, flow direction grid was calculated to determine the direction of flow for each cell in the landscape. Flow accumulation function was used to generate a drainage network for the selected pour points. The Snap Pour Point tool was used to ensure selection of points of high accumulated flow and finally, watersheds were automatically delineated. ArcGIS 10.3.1 hydrological tools and Stream Order function with Strahler method (Strahler, 1957) were used to determine stream ordering from the river

networks. Elevation models were harmonized by resampling the DEM layers into 10 m pixel size. River networks were then determined again and stream ordering calculated.

Land cover was assessed from classifies satellite imagery separately for Taita Hills, Kasigau and Sagala. For Taita Hills, the land cover classification was based on a 20 × 20 m resolution SPOT 4 satellite image from 23 October 2011 (CNES, 2013). The satellite image was classified into 9 land cover classes (Pellikka *et al*., 2017; Appendix A in the supplementary material) using an object-based approach (Benz *et al*., 2004) following the methodology presented in Clark and Pellikka (2009). Segmentation and classification was implemented in the eCognition software (Trimble). After manual corrections, the overall accuracy of the land cover map was 71.1% when comparing the map with 305 random ground-truth points.

For Sagala area, Sentinel-2A MSI Level-1C satellite image from 8 October 2016, downloaded from the Sentinel's Scientific DataHub (ESA, 2015) and RandomForest (Breiman, 2001) classifier in R software were used to create the land cover classification. Firstly, Sentinel-2A was DOS1 atmospheric corrected using Semi-Automatic Classification Plugin in QGIS. Then, classifier training areas were on-screen digitized from very high-resolution (1 m pixel size) image mosaic from 2004 and from more up to date satellite imagery (Google Earth, 2016). Then, reflectance values from the four bands blue, green, red and infra-red from the Sentinel 2A satellite image were used as the predictors for RandomForest classifier. The image was classified to the following relevant classes: bush, fields, forest and impervious.

For the Kasigau area, information from the same Sentinel 2A satellite image was combined with canopy height model (CHM) and DEM derived from the ALS data for creating the land cover classification map. First, the CHM was reclassified to 5 elevation classes in ArcGIS 10.3.1. NDVI (normalized difference vegetation index) values derived from the Sentinel-2A satellite image were used to separate non-vegetated areas from different type of green areas. Then, Kasigau study area was classified into highland and lowland zones based on the 1 m pixel size DEM to separate montane

267 vegetation from lowland vegetation after which ArcGIS Map Algebra tool was used to derive land
268 cover classes listed in Appendix A in the supplementary material. The resulting land cover map was
269 evaluated using GPS field measurements, very high resolution airborne imagery (1 m pixel size) and
270 also the previous knowledge of the area. Prior to statistical analyses, the land cover classes of the 6
271 sampling sites from Sagala and Kasigau were equated with those classified from Taita Hills. Finally,
272 zonal statistics of the percentages of land use and land cover classes were calculated for different
273 watershed areas based on the land cover layers and delineated watersheds for the whole study region.

274

275 **2.5. Statistical analyses**

276 Prior to analyses, explanatory variables measured as percentages were arcsine-transformed while
277 other explanatory variables were log-transformed. In addition, diatom abundance data were Hellinger
278 transformed to better meet the requirements of linear ordination methods (Legendre and Gallagher,
279 2001). Correlations between explanatory variables were tested using Pearson correlation. As none of
280 the correlations exceeded 0.70, we kept all the explanatory variables in the subsequent models
281 (Dormann *et al*., 2013).

282 Failure to notice spatial autocorrelation can lead to false interpretations of environmental variables'
283 effects on community composition. Thus, spatial autocorrelation of the local environmental variables
284 and species richness was tested using function correlog in the R package 'pgirmess' (Giraudoux,
285 2015). The significance of the correlogram was tested at level $P \leq 0.05$ with applied Bonferroni
286 correction (P/k, where k is the number of distance classes used). Here, distance class of 7 km was
287 used as it was most suitable for the spatial distances in our data.

288 To test whether more species are found from the tropics than boreal areas (Q_1), species accumulation
289 curves (function specaccum in the R package 'vegan′; (Colwell and Coddington, 1994; Palmer,
290 1990)) were used. The used boreal stream diatom data are explained in detail in Jyrkänkallio-Mikkola

291 *et al*. (2017). To standardize the number of sampling sites, 67 samples from the boreal data originally
292 comprising 105 sites were chosen. First order Jackknife method was used to estimate the total species
293 richness for both biomes.

294 To model spatial structures among tropical study sites, distance-based Moran´s eigenvector maps
295 (dbMEM) derived from spatial coordinates (function dbmem in the R package 'adespatial'; (Dray *et*
296 *al*., 2017)) were used. Threshold value was calculated using function give.thresh. Only eigenvectors
297 with positive autocorrelation were used to model spatial effects in subsequent analyses.

298 Redundancy Analysis (RDA) was applied to study community structure (abundance data)-
299 environment (excluding land use) relationships (Q_2) for the whole tropical dataset (Legendre and
300 Legendre, 2012). Another RDA was conducted exclusively for 39 independent sites (i.e., sites that
301 had independent catchments) to examine the effects of land use and catchment size on the diatom
302 communities. Stepwise model (forward selection) with 200 permutations was used to create final
303 RDA models (function ordiR2step in the R package 'vegan'; (Oksanen *et al*., (2015)).

304 Distribution of biodiversity across stream orders (Q_3) was studied with a set of analyses. To study the
305 uniqueness of diatom community composition across sites, local contribution to beta diversity
306 (LCBD) was calculated for each site (function beta.div in the R package 'adespatial'; (Legendre and
307 De Caceres, 2013)). The analysis was based on abundance data for which Hellinger dissimilarity
308 coefficient was applied and the analysis was run with 999 permutations. Linear regression was applied
309 to study the relationship between species richness and LCBD across sites and how richness and LCBD
310 varied across stream orders. To study whether different dissimilarity components govern diatom beta
311 diversity across stream orders, species turnover, nestedness and total beta diversity were calculated
312 for two groups of stream orders, 1-2 and 3-5, respectively (function beta.multi in the R package
313 'betapart' (Baselga *et al*., 2017)).

To explain variation in species richness and LCBD using environmental variables (Q_4), boosted regression trees (BRT; function gbm in R package 'gbm', (Elith *et al*., 2008)) were used. Tree complexity was set to 3, learning rate to 0.001 and bagging fraction to 0.75. The benefits of this machine learning technique include, that it can be run with raw values, it takes into account interactions between predictors and has small prediction errors (Elith *et al*., 2008).

Test of homogeneity of dispersion (PERMDISP, function betadisper in the R package 'vegan' (Anderson, 2006; Anderson *et al*., 2006)) was applied to relate environmental heterogeneity (habitat variables) within stream orders with corresponding variation in diatom community composition (Q_5). Sørensen coefficient was used for presence-absence data and Euclidean distances were applied for standardized habitat variables. PERMDISP tests among group differences from individual observation to their group centroid using ANOVA F-statistics (Anderson *et al*., 2006). Null hypothesis that there is no difference in diatom beta diversity and environmental heterogeneity among the different stream orders was tested. All tests were run using 999 permutations. Finally, null hypothesis that there is no relationship between the degree of beta diversity and the degree of environmental heterogeneity across the different stream orders was tested using linear regression.

Explained variation in RDA and linear regressions were reported using adjusted R^2- values. All analyses were conducted in R version 3.2.2 (R Development Core Team, 2013) using packages ´adespatial' (Dray *et al*., 2017), ´betapart´ (Baselga *et al*., 2017), 'corrplot' (Wei and Simko, 2016), 'dismo' (Hijmans, 2015), 'gbm' (Ridgeway, 2013), 'pgirmess' (Giraudoux, 2015) and 'vegan' (Oksanen *et al*., 2015).

3. Results

Altogether 297 taxa were identified from 67 tropical sites, of which 104 were found from only one site. Local diatom species richness varied from 15 to 71 in the tropical data set. The random selection

of 67 sampling sites from comparative boreal dataset resulted in taxa richness of 303. Species accumulation curves revealed that there was only a minor difference in the proportion of total species richness for boreal (76.4%) and tropical (74.6%) datasets (Q_1; Appendix B in the supplementary material).

Out of local environmental variables, only water temperature and stream width showed significant spatial autocorrelation on short distances (Appendix C in the supplementary material). Species richness showed no spatial autocorrelation. dbMEM returned one spatially autocorrelated eigenvector (referred henceforth as MEM1), that was used to model spatial structures among sites in the subsequent RDA and BRT analyses.

In the first RDA (67 sites), forward selection method returned seven significant ($P < 0.05$) variables which together explained 15.6% of the total community variation (Q_2, Fig.2a). Conductivity and pH were among the most important variables for diatom composition. Also the physical variables (shading and gravel), spatial (elevation and MEM1) and stream order were among the significant variables structuring the community. The first RDA-axis divided the sites with high conductivity, pH and high stream order opposite to those with high elevation. The second RDA-axis was mostly related to shading. We further tested whether removing singletons would increase the explained variation in community composition. This resulted only to minor increase (15.9%) of the explained variation with the same explaining variables. When presence-absence data were used explanatory power decreased to 10.9%. In the second RDA (39 sites) including land use variables, selection method returned four ($P < 0.05$) significant variables which explained 14.4% of the total community variation (Q_2, Fig. 2b). The first RDA-axis divided the sites to those with high percent of broad leaved forest and high elevation opposite to those with high conductivity.

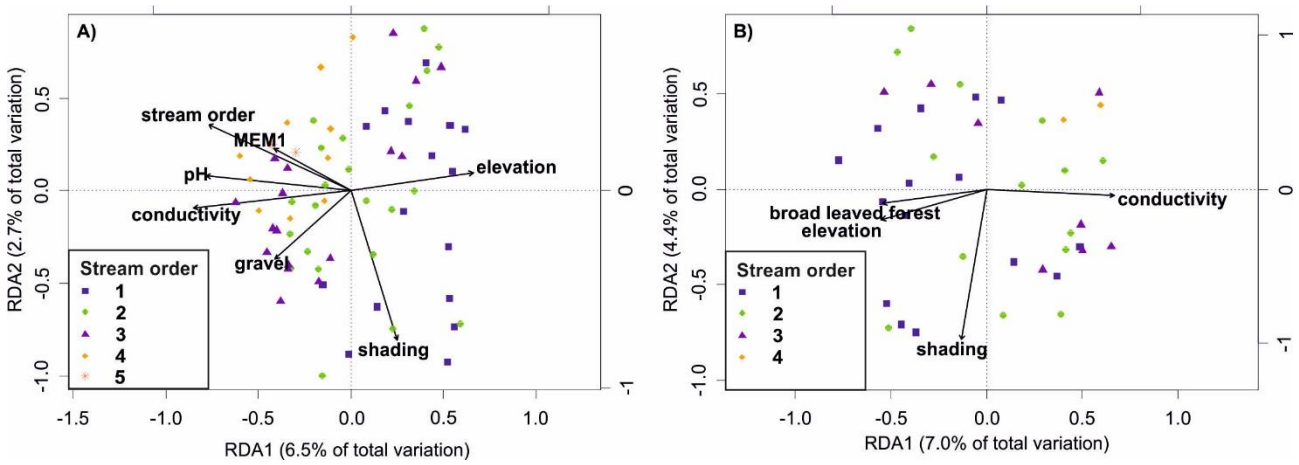


Figure 2 Ordination plots for redundancy analysis for A) all 67 sampling sites and environmental variables and B) for 39 sites with independent catchment areas and environmental and land use variables. Both ordination plots are based on Hellinger transformed diatom abundance data. Arrows represent the significant environmental variables. The explained variation is based on adjusted R^2. Abbreviations: MEM1 (spatial eigenvector derived from distance-based Moran´s eigenvector maps)

According to linear regression, species richness increased significantly with increasing stream order (Q_3, Fig.3a, $P < 0.001$, $R^2 = 0.142$), whereas LCBD values showed an opposing trend with the highest values in headwater streams (Q_3, Fig.3b, $P < 0.05$, $R^2 = 0.053$). LCBD and species richness showed significant negative relationship (Q_3, Fig. 3c; $P < 0.001$, $R^2 = 0.425$). Total beta diversity was higher in headwater streams (Q_3, orders 1-2, $\beta_{sor} = 0.933$) than in higher order streams (orders 3-5, $\beta_{sor} = 0.867$). Beta diversity components varied across stream orders. As we expected, species turnover was higher in headwater streams (orders 1-2, $\beta_{sim} = 0.905$) than in higher order streams (orders 3-5, $\beta_{sim} = 0.860$), whereas nestedness was lower in headwater streams ($\beta_{nes} = 0.027$) than in higher order streams ($\beta_{nes} = 0.036$).

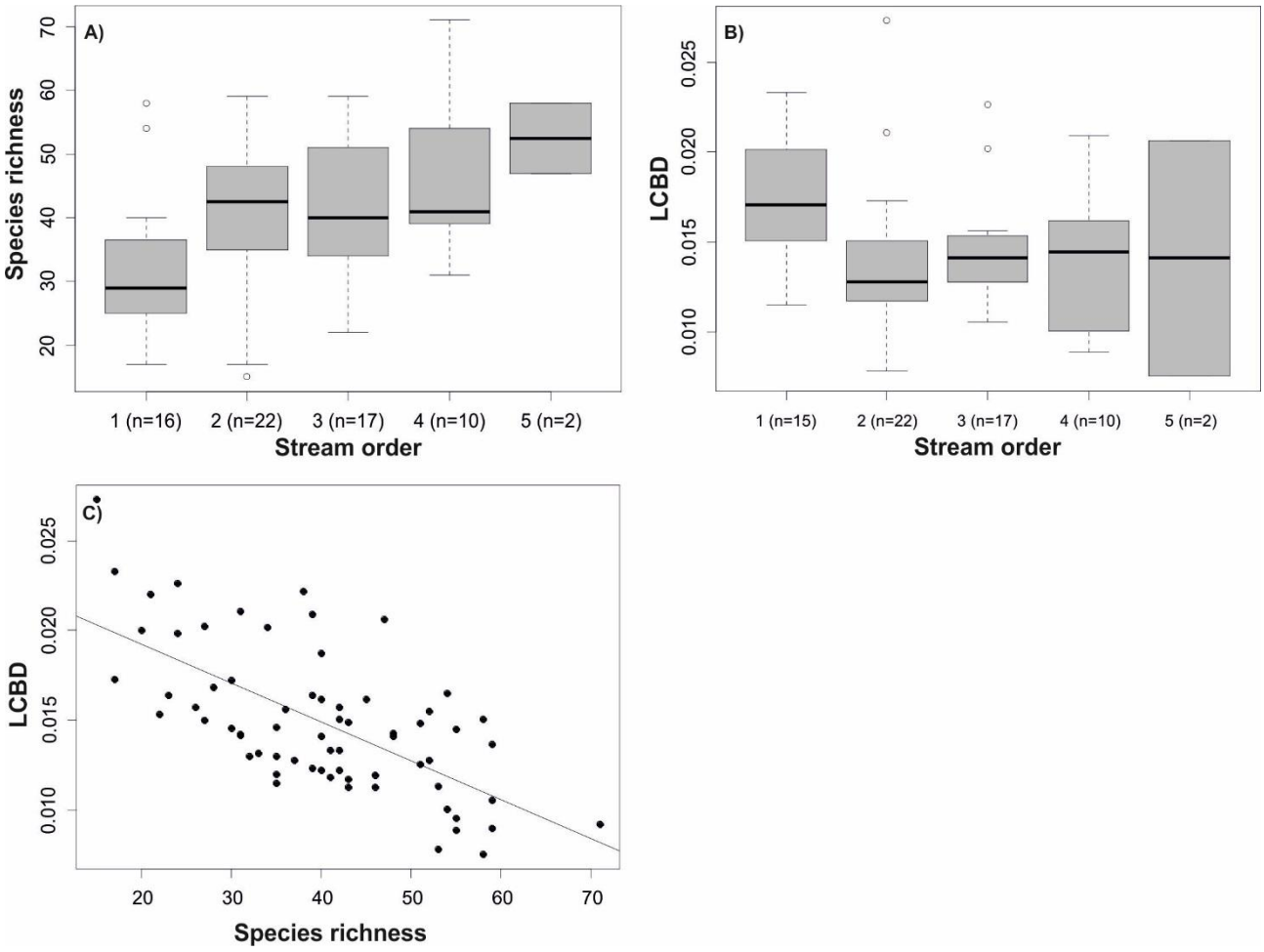


Figure 3 Boxplots representing the relationship between A) species richness and B) LCBD values and stream orders. Also shown is C) the linear relationship between LCBD and species richness. Abbreviations: LCBD (local contribution to beta diversity).

In BRT, the most important factors affecting species richness were pH, temperature, conductivity and spatial variable (MEM1) all of which showed positive relationship with species richness (Q_4, Fig.4a). Here, we also used polynomial regression and found that the relationship between species richness and temperature was unimodal ($P < 0.01$, Adj. $R^2 = 0.148$). According to BRT, the most important variables affecting LCBD were conductivity, temperature, water color and stream velocity (Q_4, Fig.4b). Conductivity, temperature and, pH were negatively related with LCBD, whereas water color scaled positively with LCBD (Fig. 4b).

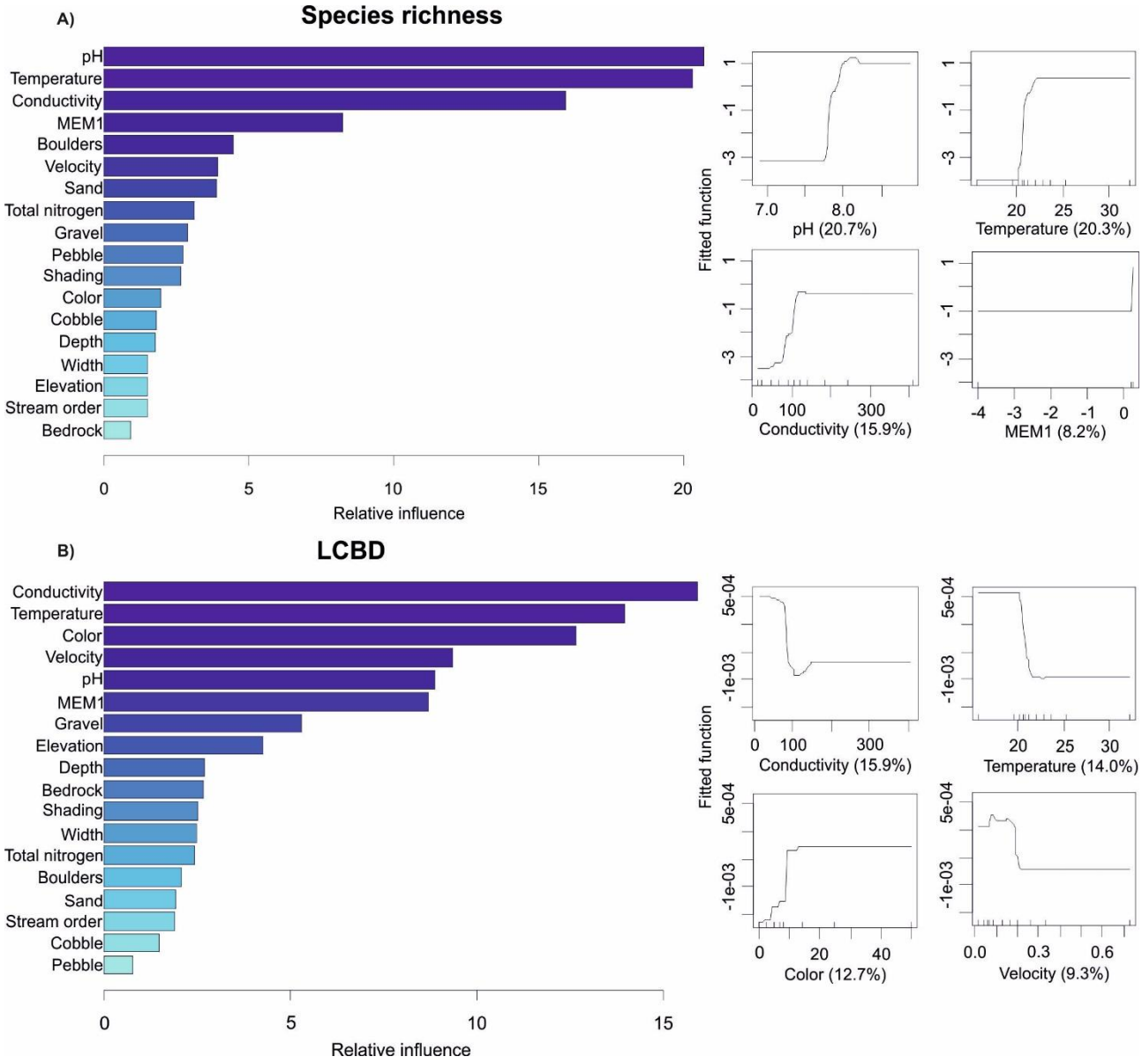
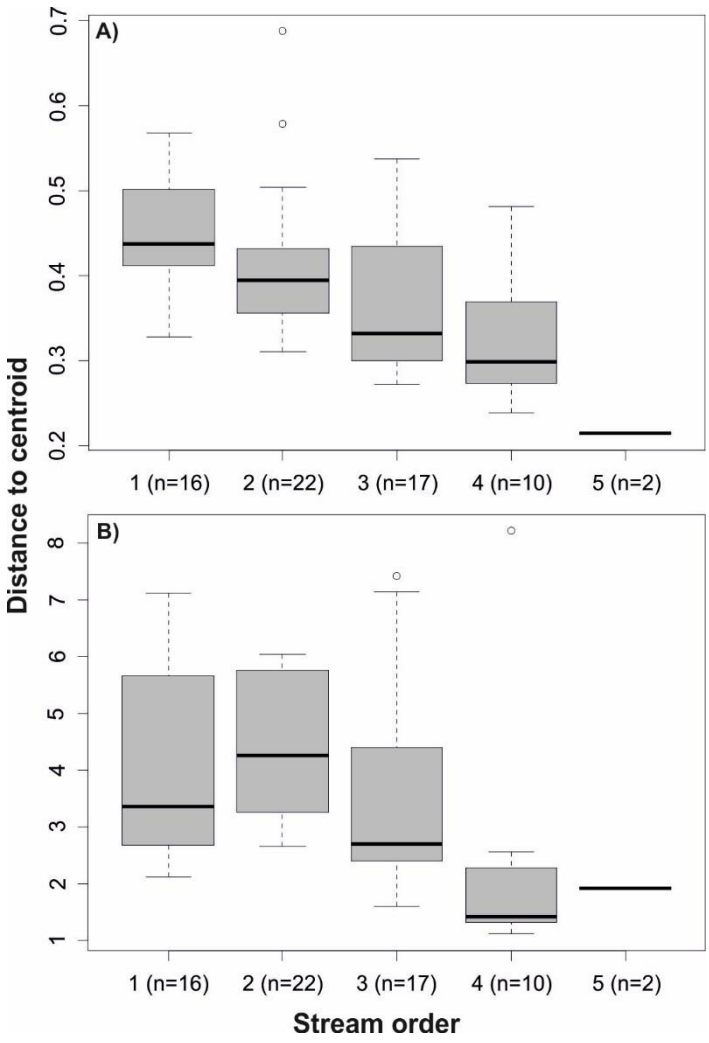


Figure 4 Boosted regression tree summary showing the relative importance of each variable and related fitted function curves for the four most important variables on A) species richness and B) LCBD values. Abbreviations: LCBD (local contribution to beta diversity), MEM1 (spatial eigenvector derived from distance-based Moran´s eigenvector maps)

PERMDISP revealed that there were significant differences in the degree of beta diversity ($P < 0.01$, $F = 6.55$) and environmental heterogeneity ($P < 0.05$, $F = 3.30$) among the stream orders (Q_5, Fig.5a, b). Beta diversity and environmental heterogeneity were higher in headstreams than in higher order streams (Q_5, Fig.5a, b). Albeit based on only five observations, we found a significant positive

398 relationship ($P < 0.05$, $R^2 = 0.736$) between the degree of beta diversity and environmental
399 heterogeneity.



400

401 Figure 5 Boxplots representing the relationship of mean distances from group centroids and stream order based on
402 homogeneity of dispersion analysis. Shown are diatom community compositional data using presence/absence and
403 Sørensen dissimilarity (A) and environmental data using Euclidean distance (B).

404

405 **4. Discussion**

406 The tropical studies focusing on diatom community structure, species richness and beta diversity
407 patterns and their underlying processes are still rare compared with the temperate and boreal studies.
408 In addition, diatom diversity patterns along stream networks are also generally relatively poorly
409 understood. Here, our results shed light on the patterns and controlling factors on these important and
410 understudied issues and may be relevant for watershed management and biomonitoring.

411 Even if largely similar sampling methods and efforts were used, we revealed no clear differences in
412 diatom species richness between tropical and boreal areas. As the sampling area of the boreal dataset
413 was larger than the tropical, and as species richness usually increases with the size of the sampling
414 area, we further tested the difference in species richness between boreal and tropical areas by choosing
415 only the 67 southernmost sites of the boreal dataset in order to have more comparable sampling areas.
416 This approach resulted in total species richness of 298 in boreal data set and the proportion of total
417 species richness on species accumulation curve in 77.9%, which indicates that tropical and boreal
418 streams seem not to differ in diatom species richness. Earlier literature about latitudinal diatom
419 richness patterns have documented very variable richness gradients. Passy (2010) found the
420 relationship of benthic diatom richness and latitude to be U-shaped in a study that comprised running
421 waters of continental U.S.. Highest species richness was found from subtropics and temperate
422 sampling sites and was related with nutrient resources rather than climate. A positive relationship
423 between marine diatom species richness and decreasing latitude was found by Salinas *et al*. (2015),
424 whereas Hillebrand and Azovsky (2001) found no latitudinal effect for diatom species richness and
425 suggested that latitudinal diversity gradient is determined by body size. Hence, our results add to the
426 controversy of the subject and call for further investigation in different types of ecosystems.

427 Our results are congruent with previous studies suggesting that diatom communities are shaped by
428 both environmental and spatial factors (Gothe *et al*., 2013; Heino *et al*., 2012; Heino *et al*., 2014;
429 Potapova and Charles, 2002; Soininen *et al*., 2016; Verleyen *et al*., 2009) indicating both
430 environmental control and dispersal limitation. However, it cannot be excluded that the observed
431 spatial structure here was caused by mass effects (i.e. due to high dispersal rates, a species can be
432 present also in unfavorable sites, (Shmida and Wilson, 1985)) rather than dispersal limitation, due to
433 the relatively small spatial scale (i.e. < 100 km) of the study and high connectivity among sites
434 (Astorga *et al*., 2012). In such conditions, mass effect may be caused by downstream drift of diatom
435 cells (Gothe *et al*., 2013).

436 Among local factors, our study highlighted the importance of water pH and conductivity for diatoms.
437 Conductivity (Astorga *et al*., 2012; Bere and Tundisi, 2011; Biggs, 1995) and water pH (Bere and
438 Tundisi, 2011; Soininen *et al*., 2004; Telford *et al*., 2006) have been repeatedly found to be important
439 controlling factors for diatoms also earlier in wide range of study regions, suggesting that these water
440 chemistry factors are important for diatoms both in tropical and boreal regions. In addition, shading
441 proved to be another important variable structuring diatom communities, a finding, that is further
442 supported by Carpenter and Waite (2000), for example. Thus, although water chemistry plays an
443 indisputable part in structuring diatom communities, it seems that also physical variables may be
444 important, especially light conditions and the substrate of the stream bed. As similar findings emerged
445 in boreal region as well (Jyrkankallio-Mikkola *et al*., 2016; Jyrkänkallio-Mikkola *et al*., 2017), the
446 importance of physical variables in structuring diatom communities applies also to the tropics, which
447 could be important to take into account in biomonitoring.

448 As expected, land use affected diatom communities indirectly through water chemistry and our results
449 suggest that forested high elevation sites including montane cloud forests harbored different diatom
450 communities compared to those found at sites with high conductivity. Similar findings have also been
451 reported by Carpenter and Waite (2000). Thus, including land use variables when unravelling factors
452 controlling the diatom communities may be useful, since this approach provides long-term
453 information of the surrounding habitat in addition to snapshot proximate controlling factors, i.e. water
454 chemistry (Bere and Tundisi, 2011; Jyrkänkallio-Mikkola *et al*., 2017). This finding also emphasizes
455 the importance of montane cloud forests for regional aquatic diversity, and furthermore their
456 conservational importance in general as they are of great importance to regional tree diversity, for
457 example in the Taita Hills (Aerts *et al*., 2011; Schafer *et al*., 2016) and are currently the most
458 threatened and one of the least studied tropical ecosystems (Williams-Linera, 2002).

459 The low explanatory power of direct ordination analyses such as RDA used here is common in
460 microbial studies (Beisner *et al*., 2006; Heino *et al*., 2012; Nabout *et al*., 2009). This might be related

461 to some unmeasured environmental variables although we find this explanation unlikely, since
462 probably the most influential factors structuring diatom communities were included in the analyses.
463 However, we admit that the inclusion of phosphorus might have increased the explanatory power of
464 the model. The surprisingly low phosphorus levels observed might be related to the fact that
465 phosphorus is a major limiting nutrient in old tropical soils (Reich and Oleksyn, 2004) and hence the
466 subsequent leach to the streams may be very low. The low explanatory power might also be due to
467 snap-shot measurements of the local environmental variables, which may not have reflected the
468 prevailing environmental conditions well enough. Indeed, the preceding amount of precipitation may
469 have had an effect on flow conditions, and subsequently, to the diatom community composition.
470 Community assembly mechanisms might also vary for example between generalists and specialists,
471 which may hinder the interpretation of environmental and community relationships (Lindstrom and
472 Langenheder, 2012).

473 As hypothesized, diatom species richness increased with stream order, which is also supported by
474 previous diatom studies (Sherwood *et al*., 2000; Stenger-Kovacs *et al*., 2014). Due to the lack of
475 stream sites above order 5, we cannot rule out the possible decrease in species richness in very large
476 streams and thus, the predicted unimodal pattern of species richness along the river network (RCC
477 theory). However, even if headwater streams harbored lower species richness they comprised more
478 unique communities than higher order stream sites. Headwater streams can be regarded as isolated
479 and less connected habitats compared to downstream sites and hence, the connectivity of the sampling
480 sites may have a strong effect on the community composition via the exchange of individuals (Lopes
481 *et al*., 2014). High uniqueness of headwater assemblages have also been reported for
482 macroinvertebrates (Finn *et al*., 2011), fish (Paller, 1994) and biofilm assemblages (Besemer *et al*.,
483 2013), stressing the conservational importance of headwater streams, contributing strongly to
484 regional gamma and beta diversity. Our results provide evidence that the high uniqueness of
485 headwater communities prevails also in the tropics, perhaps indicating that there are certain general

rules for predicting biodiversity (Finn *et al*., 2011). This result is especially important in areas, where major changes in land use occur together with climate change and consequent draughts may deteriorate or even destroy fragile and important ecosystems such as montane forests. We note that our results are in contrast with the RCC view of headwaters harboring communities less important for stream biodiversity and hence, we think that our results are also important for stream ecology in general.

Agreeing with our findings, similar negative pattern between community uniqueness and species richness across sites has also been found in several biomes and for different organisms; tropical Brazil for dung beetles (da Silva and Hernandez, 2014), subtropical China for plants (Qiao *et al*., 2015), temperate France for phytoplankton (Maloufi *et al*., 2016) and boreal Sweden for macroinvertebrates (Heino *et al*., 2017). Although Legendre and De Caceres (2013) point out that this negative relationship is not general or obligatory (see paper supporting this view for bacteria in the Canadian subarctic by (Comte *et al*., 2016)), it seems to be a relatively common phenomenon at least. Furthermore, this finding suggests that species richness may not be the only or even the best diversity measure for conservational efforts (Dormann *et al*., 2007), whereas community uniqueness might be in some circumstances more effective in this regard. We thus think that the combination of different metrics would probably be most informative approach in many ecosystems.

Of beta diversity components, species turnover was dominating, whereas nestedness was notably smaller. Similar results have been reported also by Wetzel *et al*. (2012) and Piano *et al*. (2017). In our study, it is probable that the high number of singletons contributed to the high turnover rate among sites while richness differences had smaller influence. Total beta diversity and species turnover were higher in headwater streams, whereas nestedness component increased downstream, as we expected. This finding may suggest that the increase of anthropogenic influence downstream changes also the relative effects of mechanisms contributing to beta diversity, thus supporting the results of Gutierrez-Canovas *et al*. (2013). Whereas conductivity, temperature and pH were included into the top five

most significant variables affecting species richness and LCBD, stream order played a minor role. As BRT takes into account interaction effects between variables, this finding suggests that conductivity, pH and water temperature were among the proximate factors causing the differences in diatom community composition between stream orders, as all these variables showed significant positive relationship with the stream order (Appendix D in the supplementary material). Thus, this finding is congruent with Stenger-Kovacs *et al*. (2014) who suggested that the stream order may act as a useful parameter summarizing the physical habitat in streams.

As hypothesized, diatom beta diversity and environmental heterogeneity were higher in headwater streams than in larger stream sites. Thus, our results provided evidence that along with a stronger dispersal limitation in headwaters, environmental heterogeneity may have promoted variation in diatom community composition in headwaters, suggesting that decreasing environmental heterogeneity downstream may at least partly cause subsequent decrease in diatom beta diversity towards larger streams. The higher environmental heterogeneity in headwater streams stresses their conservational importance for regional diversity, which gets support from other studies that have found higher habitat heterogeneity to increase beta diversity for planktonic diatoms (Zorzal-Almeida *et al*., 2017) and phytoplankton in general (Maloufi *et al*., 2016). Although we admit that the conservation of microbial organisms may not have as strong research need as conservation of larger taxa, similar results have also been reported for stream macroinvertebrates (Astorga *et al*., 2014) emphasizing the effect of environmental heterogeneity to regional diversity. Consequently strong emphasis should be placed on headwater stream conservation and management in general.

5. Conclusions

Our results indicate that tropical streams do not seem to harbor more diatom species compared to boreal streams. Studies aiming to unravel the determinants of diatom communities are encouraged to

consider spatial, land use and physical variables in addition to water chemistry variables. Land use variables may affect diatom communities indirectly through water chemistry and can provide long term information of the surrounding habitat. Diatom species richness and the uniqueness of the communities may vary across stream orders with headwater sites encompassing more unique communities and higher order streams higher species richness. This results is important to take into consideration in biomonitoring and studies focusing on stream diatom species richness and community composition. Environmental heterogeneity seems to be higher in headwater streams and also relate with the degree of diatom beta diversity and, thus, our results emphasize the management and conservational importance of headwater streams.

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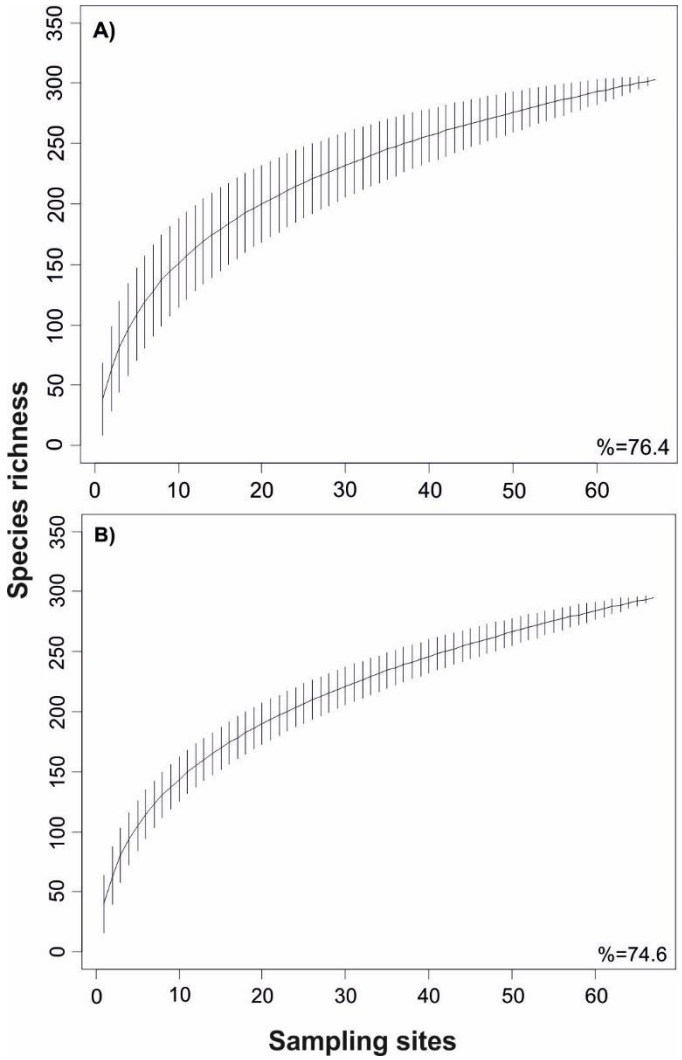
840

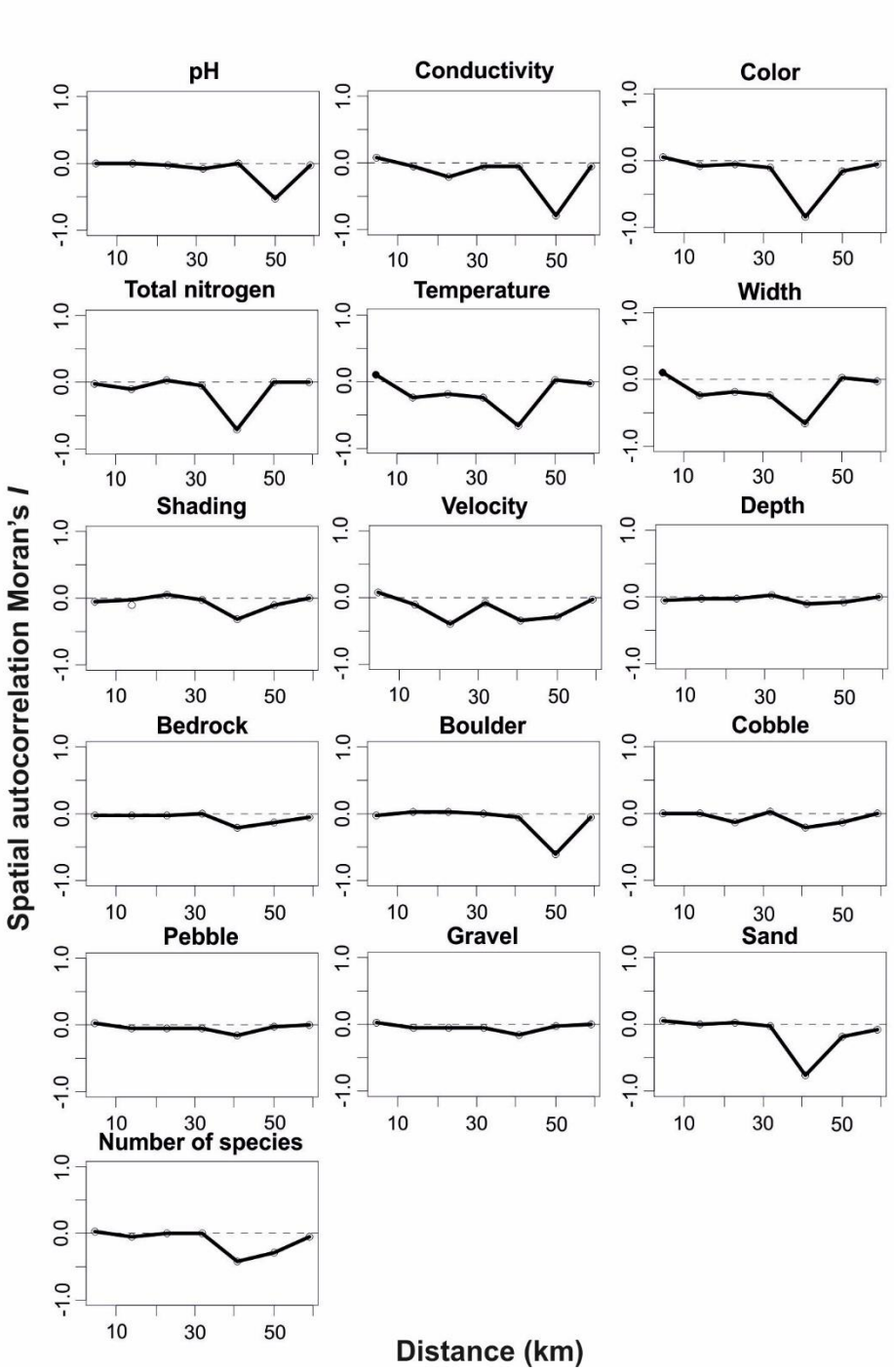
841 Appendix A List of measured environmental and land use variables (average values and ranges). * removed from
842 multivariate analysis due to low concentrations, **removed from further analysis to avoid 100 % coverage of the
843 variable group.

	Variable	Mean values	Range
Environmental variables (n=67)	Elevation (m)	1293.00	(713.00 – 1929.00)
	pH	7.90	(6.90 – 8.89)
	Conductivity (mSm^{-1})	120.28	(15.10- 408.70)
	Colour (Pt mgl^{-1})	9.02	(0 - 50)
	Total P(μgl^{-1}) *	14.46	(<10.00 – 69.00)
	Total N (μgl^{-1})	698.06	(150.00 – 2380.00)
	Shading (%)	40.11	(0.00 – 96.30)
	Depth (m)	0.07	(0.01 - 0.23)
	Width (cm)	148.01	(17.00 – 1310.00)
	Velocity (ms^{-1})	0.17	(0.02 - 0.73)
	Sand (%)	46.17	(0.00 - 100.00)
	Gravel (%)	5.29	(0.00 – 46.50)
	Pebble (%)	4.66	(0.00 – 35.00)
	Cobble (%)	7.34	(0.00 – 49.50)
	Boulders (%)	9.11	(0.00 – 64.00)
	Moss (%)**	5.73	(0.00 – 90.00)
Land use variables (n=39)	Catchment area (km^2)	2.32	(0.14 – 25.58)
	Cropland (%)	38.00	(0.00 – 77.76)
	Shrubland (%)	1.93	(0.00 – 23.81)
	Thicket (%)	5.75	(0.00 – 39.14)
	Woodland (%)	21.10	(0.00 – 51.42)
	Plantation forest (%)	15.75	(0.00 – 41.56)
	Broadleaved forest (%)	14.70	(0.00 – 93.00)
	Bare soil and built areas (%)	1.10	(0.00 – 14.00)
	Bare rock (%)	1.50	(0.00 – 15.60)
	Water bodies (%)**	0.01	(0.00 – 0.41)

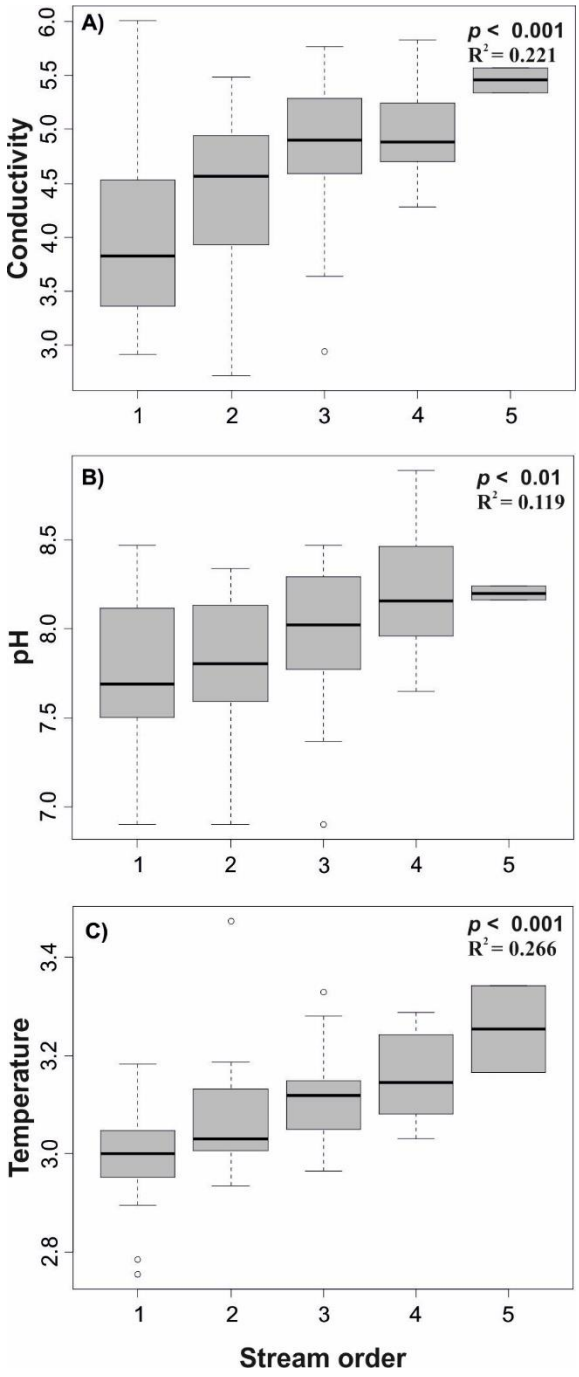
844



Appendix B Species accumulation curves for A) boreal and B) tropical streams. The proportion of estimated species richness that 67 sampling sites covered is shown on the lower right corner.



Appendix C Moran's I correlogram representing spatial autocorrelation for 15 environmental variables and diatom species richness. Black filled circles mark significant values of Moran's I and represent significant positive autocorrelation.



Appendix D Boxplots representing the relationship of A) log transformed conductivity, B) pH, C) log transformed temperature and stream order.